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Effects of Fire on Fauna

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State-of-Knowledge Review
Fire Effects Workshop

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EFFECTS OF FIRE ON FAUNA

A State-of-Knowledge Review

Prepared for the Forest Service
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CONTENTS

	Page
Foreword	iv
Introduction	1
Faunal Influence on the Probability of Fire	2
Direct Effects of Fire on Fauna	2
Vertebrates	2
Invertebrates	3
Indirect Effects of Fire During an Animal Lifetime	6
Terrestrial Fauna	6
Stream Fauna	8
Habitat Modification Effects on Populations	9
Evolution of Species in a Fire Environment	14
Knowledge Gaps, Research Needs, and Priorities	15
Summary and Conclusions	15
Literature Cited	17

FOREWORD

Recent changes in Forest Service Fire Management Policy make it clear that resource managers today need a great deal more information on the physical, biological, and ecological effects of fire. They will need information on fire behavior and fire effects as a basis for analyzing the benefits, damages, and values of various fire management alternatives. Managers must be able to place a value on all resources if they are going to incorporate fire and its effects into land management plans. The Forest Service is committed to the concept that fire management planning has to be a fundamental part of all our planning.

Recent laws and regulations also give additional guidance for the Forest Service to use in developing land management plans for each unit of the National Forest System. These plans must coordinate outdoor recreation, range, timber, watershed, wildlife and fish, and wilderness resources. Interdisciplinary planning is vital, and research must cover the same universe as our planning--therefore interdisciplinary research is a must.

The effects of fire have been studied since the beginning of organized Forest Service research, but the results are scattered over a wide range of outlets. In addition, research is conducted on the effects of fire under several appropriation line items, and in some instances lacks the interdisciplinary approach needed to make the results as useful as possible to land managers.

The National Fire Effects Workshop was held April 10 through 14, 1978, as a first step in responding to the most recent changes in policies, laws, regulations, and initiatives. One of the major Workshop objectives was to prepare a report indicating the current state of knowledge about effects of fire on various resources. These reports formed the basis for pinpointing knowledge gaps. Using this information and input from land managers, priorities for research needed on the effects of fire were established.

Six work groups were formed to prepare the effects of fire state-of-knowledge reports on the following: soil, water, air, flora, fauna, and fuels. Work group members were mainly Forest Service research scientists, but individuals from National Forest Systems, Bureau of Land Management, National Park Service, Fish and Wildlife Service, and Bureau of Indian Affairs also participated.

We hope these state-of-knowledge reports will prove useful to researchers and research planners as well as land and fire management planners. Each report will be published as an individual document. A separate bibliography will be included in this series in an effort to provide a source document for most of the literature dealing with the effects of fire.

EFFECTS OF FIRE ON FAUNA

A State-of-Knowledge Review

INTRODUCTION

In preparing a state-of-knowledge review for fire and fauna, our basic reference source was the chapter "Effects of Fire on Birds and Mammals," by J. F. Bendell (1974) in the book "Fire and Ecosystems". In addition to summarizing this 52-page paper, we added material covering invertebrates and stream fauna and attempted to recognize additional references published since 1974. In total, the material presented here summarizes about 450 citations.

One of the major problems in attempting any generalization about the effects of fire on fauna is the variation in fires: intensity, duration, frequency, location, shape, extent, season, fuels, sites, soils, and prescribed fires as compared to wildfire. Few studies are quantitative, have adequate controls, and have been carried on long enough to really assess effects on fauna. Another complicating factor is that much of the information about fire effects on fauna actually reports plant community modification by fire and the consequent influence on food, cover, and habitat used by various faunal species.

The effects of fire on fauna can be organized in a variety of ways, but one logical sequence is provided in the time series established by the fire:

- (1) Prior to any burn, some faunal species influence the probability that a fire will occur at all.
- (2) During the active combustion stages some faunal species are killed, but many exhibit predictable behavioral characteristics in the presence of fire.
- (3) The condition of the immediate post-fire environment leads to further specific behavioral responses within faunal populations.
- (4) Over a longer period of time, plant community development influences population levels, survival and reproduction of most faunal groups.
- (5) And finally, in environments subjected to repeated fires, species evolution leads to common characteristics shared by many faunal groups.

FAUNAL INFLUENCE ON THE PROBABILITY OF FIRE

Several years ago, Robert Mutch (1970) suggested that many plant species have characteristics that enhance flammability of the communities in which they occur. Presumably, animal species that benefit from fire may also exhibit such characteristics. The evidence is mostly circumstantial, but animals may influence the action of fire in ways that perpetuate their habitat.

The most frequent natural start of fires is by lightning (Komarek 1968, Kourtz 1967, Taylor 1969). Squirrels may mutilate the tops of trees (Keith 1965) and influence the likelihood of lightning strike. The piles of cone scales created by squirrels (Rowe 1970), and fine woody material in nests of woodpeckers may make excavated trees more susceptible to burning. Fire-tolerant and fire-sensitive conifers are well documented (Flieger 1970, Kayll 1968, Knight and Loucks 1969, Rowe 1970), and with some exceptions, herbivores tend to suppress fire-sensitive species and release the more flammable varieties (Dasmann 1971, Pimlott 1963, Bergerud and Manual 1968, Brink and Dean 1966, Radvanyi 1970, Ahlen 1968). In addition, wild animals may distribute seeds on new burns (Ahlgren 1960, West 1968), which very often are seeds of wildlife food plants.

Large herbivores, such as deer, elk, bison, and moose may alter the fuel in grasslands and forest to influence burning (Bailey and Poulton 1968, Flook 1964, Hansen et al. 1973, Hough 1965, Pimlott 1963, Ross et al. 1970, Jeffrey 1961). At the other extreme, it is conceivable that grazing by herbivores could reduce fuel loads in some instances. Campbell (1954) has reported that livestock grazing reduces the fire hazard by removing potential fuel and by establishing trails (firebreaks) through forested areas.

In summary, while it seems possible that some faunal species do influence the probability of wildland fires, the cumulative evidence is mostly conjectural.

DIRECT EFFECTS OF FIRE ON FAUNA

Direct effects of fire on faunal populations vary at different levels of phylogenetic development. For this presentation we have separated the discussion into sections on vertebrates and invertebrates.

Vertebrates

Immediate response of vertebrate animals to fire appears to run the gamut from wild panic through calm movement away from the fire to positive movement toward the fire. The kind of response is related to both the mobility of the animal and size of the fire with smaller rodents such as squirrels, mice, cotton rats and chipmunks most likely to exhibit panic (Udvardy 1969b, Komarek 1969, Tevis 1956). Larger, more mobile, animals such as moose, caribou, swans and raccoon usually move calmly (Hakala et al. 1971, Vogl 1973, Sunquist 1967) while many large African animals, insectivorous birds, quail, turkeys, birds

of prey and several primates appear to be attracted by fires (Phillips 1965, Komarek 1967 and 1969, Stoddard 1963). Birds generally show no fear of fire and some are even attracted to the smoking landscape. Alligators will use burned shoreline almost exclusively.

Direct mortality of animals in fires has been documented by some investigators. Bodies of small birds and voles (Hakala et al. 1971), elephants, lions, warthogs and antelope (Brynard 1971), deer, wood rats and rabbits (Chew et al. 1958) have been found in burned areas, and several investigators consider fires very destructive of wildlife (Ahlgren and Ahlgren 1960, Lutz 1956). However, other investigators have remarked on the relative scarcity of dead animals in burned areas (Stoddard 1963, Keith and Surrendi 1971, Doerr et al. 1970, Tevis 1956, Sims and Buckner 1973, Tester 1965, Komarek 1963).

Survival, particularly of small mammals, is a direct function of the great decrease in temperature in the ground only a few centimeters away from the heat of the fire (Ahlgren and Ahlgren 1960, Cooper 1961, Martin 1963, McFayden 1968, Smith 1968, Lawrence 1966). Lethal air temperature for small mammals is about 145° F (Howard et al. 1959), but when animals are killed in fires the probable cause of death is usually suffocation rather than high temperatures (Lawrence 1966, Chew et al. 1958).

In general, while some evidence of vertebrate mortality has been reported, the most common opinion is that vertebrates are rarely killed in fires and where death does occur it is usually negligible (Vogl 1967, Phillips 1965, Stoddard 1963).

Invertebrates

Effects of fire on invertebrate populations may be transitory or long lasting. In general invertebrates decrease because the animals or their eggs are killed by the flames or heat, and their food supply and shelter are diminished. In some instances flying insects are attracted by heat, smoke, or killed or damaged trees; thus populations of certain species may increase during and after a fire.

The invertebrates in the forest can be placed in two broad categories-- those that spend all or most of their lives in the forest floor or mineral soil, and those that reside in these habitats only temporarily or not at all. In the following discussion the term soil fauna will be used for the former and surface insects for the latter.

Early work on fire and soil fauna in this country was done in the South. Burning is thought to limit the numbers of ticks and chiggers because those unattached to host animals are vulnerable to fire and few can escape (Stoddard 1935). In longleaf pine stands, five times as many mites were found in unburned as compared to burned forest soils (Heyward and Tissot 1936, Heyward 1937). In the top 2 inches of mineral soil, 11 times more mites were found in

the unburned as in the burned areas. On the Duke Forest (Pearse 1943), unburned plots had more of practically all the soil fauna species than did the burned ones. But only hand sorting, without magnification, was done and thus many small animals were not examined. More recently in New Jersey (Buffington 1967), it was found that 1 year after a wildfire most soil fauna were more scarce on the burned than on the unburned areas. The exceptions were 2 species of ants that were more common on burned areas. Garren (1943) also reported soil fauna scarce in frequently burned soils.

In Idaho, the relative abundance of the soil fauna was determined 1, 2, and 3 years after clearcut areas were prescribed burned (Fellin and Kennedy 1972). In the mineral soil, the older the burn the more individuals were found; in the forest floor more animals were recovered in the oldest burn. Prescribed burning differentially affected adult and larval nematodes in a Louisiana pine stand (Harrison and Murad 1972). The total number of larvae were reduced by burning but no differences were found in adult populations. In loblolly pine in South Carolina, the populations of soil fauna were reduced by annual and periodic prescribed burning (Metz and Farrier 1973). With the periodic burns, spaced 4 or 5 years apart, populations returned to normal after 3 or 4 years. However, in this same study species diversity of collembolans was increased by both annual and periodic fires (Metz and Dindal 1975).

Prairie fires in Illinois reduced the populations of both soil fauna and surface insects over those in the unburned areas (Rice 1932): As in some other studies, ants were often found in greater numbers on the burned areas.

Results of studies conducted in other countries parallels those in this country. In Austria, mites, the most common soil organisms collected, were less abundant in burned areas (Jahn and Schimitschek 1950). In the coniferous forest of northern Sweden more mites were found in unburned than burned forest floor, but the author ascribed the difference to normal variation in their population (Forsslund 1951).

In Finland, clearcutting forests that had a thick raw humus layer and then burning the areas a year later greatly reduced the population of oribatid mites. Five years after the burn the oribatids still showed no sign of recovery (Darppinen 1957, Huhta et al. 1967 and 1969). After wildfires swept through radiata pine plantations in Australia, the soil fauna were examined on sites that had been lightly and severely burned. The populations in the severely burned areas were reduced when compared to the lightly burned ones (French and Keirle 1969). In Canada, the density of soil fauna was found to be decreased in both the forest floor and surface 5 inches of mineral soil 2 years after a slash burn (Vlug and Borden 1973). Using "fuel reduction fires" of even low intensity in Australian dry forests caused a substantial mortality of soil fauna in both the forest floor and surface soil. On these sites it was estimated that it would take from 2 to 6 years for the fauna populations to return to a prefire level (Leonard 1977).

From this brief review it is obvious that fires reduce the populations of most soil fauna. Additional research is needed to determine reinvasion and reproduction rates on burned areas. Ecological studies should be made to enable us to better understand the role of the various groups of animals in the forest. These ecological studies are very complicated due to the great variety of organisms involved, and cooperation is needed by workers in many disciplines, e.g., invertebrate zoologists, acarologists, and nematologists.

Many studies of surface insects show their numbers are reduced by fire. Fires in Australia, both prescribed and wild, reduce the populations of stick insects (phasmatids) to a very low level if the forest floor is completely consumed. Both nymphal and adult stages are affected, and the burning has a long-term depressing effect on populations (Campbell 1961). Beetle populations in an area of shrub steppe vegetation in southeastern Washington that had been burned by a wildfire were examined and compared with the populations of an unburned area. Of the four species studies, all were found in both areas, but the populations of two species were significantly reduced by burning (Rickard 1970).

The effect of burning 1-acre plots on the invertebrate component of grassland in Ohio was brief, and populations were back to normal in 3 months. Sampling was done by the vacuum method, and so few soil fauna species were involved (Bulan and Barrett 1971). In a study of this type, small plots and the mobility of the insects sampled could have masked the effects of the burning. Beetle populations in Florida pine forests that had been burned annually were compared to those which had not been burned for 10 or more years. Of the total number of carabids trapped, 85 percent were taken in the unburned plots (Harris and Whitcomb 1974). In New Jersey, the distribution of the periodical cicadas was studied in 1902 and in 1970. In the 1970 study the insects had disappeared from many of the locations where they were found earlier. This was attributed to destruction of forests, forest fires, and urbanization (Schmitt 1974). Prescribed fire in sugar maple stands in Michigan reduced the maple leaf cutter because pupae in forest floor were killed. Pupal mortality was nearly 90 percent and was higher than chemical control percentages obtained by other workers using Carbaryl (Simmons et al. 1977). In the Lake States it was found that broadcast burning was effective in controlling the red pine cone beetle in seed production areas (Miller 1978).

In addition to decreasing surface insect populations fire may also increase the numbers of certain species. This may occur during the fire or after when the insects attack the killed or weakened trees. Soon after Douglas-fir are killed by fire they may be attacked by a variety of insects. The phloem region is attacked first and then other species follow, attacking the sapwood and heartwood (Kimmey and Furniss 1943). Some insects are attracted by smoke and heat, e.g., buprestid beetles in the genus Melanophila. They are known in some areas of North Carolina as "fire bugs" and have been observed landing on stumps that were still glowing (Linsley 1943). In the southern pine region, "trees injured by fire are often very attractive to bark beetles; thus such trees not uncommonly result in large concentrations of beetles, which not only attack scorched trees, but at times attack and kill considerable surrounding

green timber" (Beal and Massey 1945). And with respect to the western pine beetle, "bark beetle populations usually concentrate in fire-injured trees surviving a fire, indicating that these trees are especially attractive to the beetles" (Miller and Keen 1960). In Mississippi it was found that insect populations on right-of-way were increased by the prescribed burning of the herbaceous vegetation. Samples were collected using the sweep and vacuum methods (Hurst 1970). A rather lengthy list of insect species attracted to forest fires by smoke and heat has been published (Evans 1971).

Whereas soil fauna seem to be killed by fire, surface insects are not at susceptible. They are protected by their ability to fly, to move quickly into tunnels in the soil, and to be insulated from heat and smoke by the bark of the trees they inhabit. Thus, insects that can be controlled by fire are usually the ones that lay eggs, or have immature forms in the forest floor. If an insect pest is to be controlled with fire, its life history must be known in detail for fire to be used at the most appropriate time.

In streams, the immediate effect of fire is rarely consequential. Direct heating of small streams (Hall et al. 1969) or accidental spill of retardant chemicals could eliminate all life from stream habitat. However, severe damage of any but short stretches of water is unlikely.

INDIRECT EFFECTS DURING AN ANIMAL LIFETIME

Terrestrial Fauna

Burned areas have their own local climate and microclimates that may affect terrestrial fauna in a number of ways. Smoke is probably of little consequence, but the black of charred vegetation and soil may effectively increase the heat input to an area and affect animal distribution (Klein 1960, Pruitt 1959). Increased light and temperature in a burn may favor ground squirrels and quail (Udvardy 1969, Hurst 1971, Gashwiler 1970, Tevis 1956) while warblers, wood mouse, and redbacked vole will avoid such areas (Brewer 1958, Kendeigh 1945, Udvardy 1969, Ahlgren 1966, Beck and Vogl 1972, Gashwiler 1970). Several other studies suggest how temperature might affect wildlife on a burned area (Brewer 1958, Cruikshank 1956, Drent 1972, Horvath 1964, Klein 1960, Pruitt 1959, Salt 1952, Udvardy 1969a).

Humidity may also determine the local distribution of birds and mammals (Henderson 1971, Pruitt 1953, Salt 1952). Blue grouse, for example, appear to select warmer and drier habitats than ruffed grouse. Cold and wet weather has been blamed for chick mortality and population decrease in several species of gallinaceous birds that live in habitats that burn (Larsen and Lahey 1958, Ritcey and Edwards 1963, Marcstrom 1960, Hoglund 1970, Shelford and Yeatter 1955). Presumably, warmer and drier burned areas would be more favorable for grouse because of nutritious early spring vegetation and increased numbers of litterdwelling insects (Siivon 1957, Gullion 1967, Watson and Moss 1972, Lovat 1911).

Increases in insect numbers is not a universally accepted hypothesis however--most studies indicate decreases. Fire alters the environment on and in the ground (Ahlgren and Ahlgren 1960, Eddleman and McClean 1969, Isaac and Hopkins 1937, Potter and Moir 1961, Scotter 1971), profoundly changes the microfauna found there (Gill 1969, Gillon 1971, Hurst 1971, Lussenhop 1971, Pearse 1943, Vlug 1972), and thereby modifies the invertebrate food supply of several species (Wing 1951, Gullion 1967). At times woodpeckers move into burns in large numbers, presumably in response to the food supply provided by the insects that attack dead trees (Blackford 1955, Koplin 1969).

Fire may also have an impressive cleansing effect in reducing the numbers of external and internal parasites that affect birds and mammals (Brynard 1971, Grange 1949, Isaac 1963, Lovat 1911, Stoddard 1931, Fowle 1944, 1946, and 1960, Bendell 1955, Jensen 1962, Casperson 1963). However, Bendell (1955) has shown that this effect is unlikely to last very long or to have any major influence on grouse populations.

Perhaps the greatest immediate change made by fire is the destruction of large trees and shrubs and resultant modification of habitat structure. This is particularly true on logged areas where some material is removed and other material left on the ground. Unburned logging slash and fallen trees have been reported as providing important centers of activity for juncos and wrens (Franzreb 1977), as a considerable obstruction to caribou deer, and elk (Kelsall 1968, Banfield 1954, Gates 1968, Lyon 1976), and as inconsequential to grouse (Redfield et al. 1970). Burning may also remove obstructions in some habitats and allow wildlife, including big game, quail and waterfowl, to move about more freely (Austen 1971, Lemon 1968, Hurst 1971, Stoddard 1931, Givens 1962, Vogl 1967 and 1969, Ward 1968).

Following burning, the deep ash, baked soil, and removal of stem and litter cover may reduce movement and burrowing by mice and voles, and prevent habitat use by sparrows and bobolinks (Tevis 1956, Cook 1959, Gashwiler 1970, Sims and Buckner 1973, Tester and Marshall 1961, Potter and Moir 1961). However, Peromyscus usually increase after fires (Sims and Buckner 1973, Tester 1965) and litter removal may make some foods more available to wildlife (Stoddard 1931 and 1963).

Frequency and velocity of winds on a burned area may increase heat loss, especially if the animal is wet (Hart et al. 1961). However, some experiments have suggested lack of cover as unimportant (Robinson 1960) while other studies have shown poorer survival and a tendency for animals to avoid open areas (Cheatum 1949, Miller et al. 1972, Kelsall 1968, Scotter 1971).

Snow depth, duration, and crusting on burns are profoundly different from those in the unburned or unlogged forest, but it is not possible to generalize about animal response to different snow conditions except in very specific situations. A number of grouse burrow in the snow and are less vulnerable where snow is deep and has no crust (King 1971, Weeden 1965, Gullion 1967,

Dorney and Kabat 1960, Pruitt 1959), but deer, moose, elk and caribou avoid deep snow (Edwards 1956, Kolenosky 1972, Pimlott et al. 1969, Kelsall and Prescott 1971, Gates 1968, Pruitt 1959, Legee and Hickey 1977) and may find the crust either desirable (Kelsall and Prescott 1971) or a nuisance (Geist 1971).

Finally, during the first growing season following a fire, early and vigorous growth of vegetation in the spring usually improves food supplies (Ahlgren and Ahlgren 1960, Anderson 1972, Daubenmire 1968, Sykes 1971, Siivonen 1957). Grazing habits and distribution of cattle, for example, are influenced by burning. Utilization is heaviest on areas most recently burned; and rotation burning can provide a grazing management system that sustains range productivity (Halls et al. 1952, Duvall and Whitaker 1964, Pearson and Whitaker 1974). Burning results in additional cattle gains (Lemon 1946). Cattle on burned ranges gain 2 to 3 times more than those on unburned range (Halls et al. 1952).

Early and vigorous vegetation growth may also influence some ground-nesting birds. Georgia quail prefer freshly burned and 1-year rough areas for late summer nesting sites (Harshbarger and Simpson 1970). Simpson (1972) showed the best burned habitat for successful quail nesting was a 1-year post burn.

In summary, the immediate post-fire environment presents all terrestrial fauna with a sudden and drastic modification of habitat structure and local microclimate. Increased light and temperature, lowered humidity, greater wind velocities, modified snow depths, and changes in food and cover may have both positive or negative influences on various faunal species.

Stream Fauna

Of great importance to stream habitat are the impacts that may occur as a result of increased soil erosion, increased water flow, removal of stream-side vegetation, and increased nutrient loading. Sediment input to streams may reduce the size of spawning gravels or deposit fine material that smother eggs, prevent emergence of fry (Cordone et al. 1961, J.W. Burns 1970b, Cooper 1965, Phillips 1961), increase predation losses and reduce populations of preferred food species (may, caddis, and stone flies) (Bjorn et al. 1977, J.E. Burns 1970a, Moring 1975).

Concurrently, eggs may be crushed or dislodged as a result of both increased flow and because reduction of gravel size as a consequence of erosional activity causes overturn to occur at lower flows. The mechanics of gravel overturn have been investigated by Bjorn et al. (1970) and impact on eggs and aelvin are suspected to be high but are not well documented. Removal of streamside vegetation often increases streambank erosion, reduces the available habitat and raises stream temperatures. And, as a result of higher temperatures, faunal oxygen demand increases while dissolved oxygen content declines.

Increased incidence of fish disease is also a normal consequence of habitat deterioration caused by increased temperature (Fish and Rucker 1945).

Increased nutrient loading of streams is also a common post-fire phenomenon. Concentrations of chemicals seldom reach toxic levels, however, and the effects on productivity are usually beneficial (Fredriksen et al. 1975). Increased algae production at the bottom of the food chain appears to sustain a greater biomass and a more diversified population of insect larvae (Fredriksen 1978. Impacts of fire on stream habitat. Office Report. Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon, 5 p.).

In summary, the most important effects of fire on stream fauna are effects related to loss of streamside vegetation and increased sediment load to the stream. Research is needed in both areas, but the major thrust appears to be a watershed research function.

HABITAT MODIFICATION EFFECTS ON POPULATIONS

Beyond the immediate influences on animals, fire is the initial stage for major long-term modifications of habitat. Obviously, food, cover, water and the total environment available are drastically modified by the disturbance. And, for a considerable number of post-fire years, plant succession will continue to produce substantial change. In general, the larger animals prized as game are reported to increase after fires. For example, moose, white-tailed and mule deer, elk, cougar, coyote, black bear, beaver, hares, turkey, pheasant, bobwhite, sharp-tailed, ruffed, red, and blue grouse, prairie chicken, willow ptarmigan, heath hen and some water fowl have been reported as benefited by fire (Dahlberg and Guettinger 1956, Edwards 1954, Grange 1949, Hansen et al. 1973, Hayes 1970, Jonkel and Cowan 1971, Kelsall 1972, Lawrence 1954, Miller and Miles 1970, Miller et al. 1966 and 1970, Mossop 1971, Stelfox and Taber 1969, Amman 1963, Lutz 1956, Spencer and Hakala 1964, Taber and Dasmann 1957, Gullion 1967, Lovat 1911, Stoddard 1931 and 1963, Vogl 1967, Zwickel and Bendell 1972, Thompson and Smith 1970).

On the other hand, fire may temporarily displace or eliminate species that are dependent on late stages of plant community development such as mountain, woodland and barren-ground caribou, marten, red squirrel, grizzly bear, wolverine, fisher and spruce grouse (Cringan 1958, Edwards 1954, Hayes 1970, Scotter 1971, Grange 1948).

Among the smaller, mostly non-game animal species, the beneficial or detrimental effects of fire are far less certain. For many species there may be no effect at all. Bendell (1974) presents a summary of 22 studies of breeding birds and mammals in burned and adjacent unburned habitat (table 1) in which he shows the remarkable stability of species numbers. Among birds, the greatest loss was from foragers of the tree trunk and canopy and the greatest gain was among ground feeders. Among mammals, the loss was in forest species and the gain in grassland and shrub forms. Overall, the result of

fire was a slightly richer avifauna and little change in numbers of mammalian species. The major difference at the species level appears to be that burns and fire-dependent forests support larger birds (Bock and Lynch 1970, Martin 1960) and mammals than unburned or relatively fire proof forests. In table 2, Bendell (1974) has summarized these same studies to indicate changes in density and population trends. Some increases and decreases are noted, but 80 percent of both mammal and bird populations of wildlife remained about the same in both density and trend.

Table 1.--Change in species of breeding birds and mammals after burning (Bendell 1974)

Foraging Zone	: Before Burn	: After Burn	: Gained ^{2/} (Percent)	: Lost ^{2/} (Percent)
Number of species of birds ^{1/}				
Grassland and shrub	48	62	38(18)	8(4)
Tree trunk	25	26	20(5)	16(4)
Tree	<u>63</u>	<u>58</u>	<u>10(6)</u>	<u>17(11)</u>
Totals	136	146	21(29)	14(19)
Number of species of mammals ^{3/}				
Grassland shrub	42	45	17(7)	20(4)
Forest	<u>16</u>	<u>14</u>	<u>13(2)</u>	<u>25(4)</u>
Totals	58	59	16(9)	14(8)

^{1/} Sources: Biswell et al. 1952, Bock and Lynch 1970, Emlen 1970, Ellis et al. 1969, Hagar 1960, Kilgore 1971, Lawrence 1966, Michael and Thornburge 1971, Tester and Marshall 1961, Vogl 1973.

^{2/} Numbers of species in parentheses.

^{3/} Sources: Ahlgren 1966, Beck and Vogl 1972, Biswell et al. 1952, Cook 1959, Gashwiler 1970, Keith and Surrendi 1971, Lawrence 1966, LoBue and Darnell 1959, Sims and Buckner 1973, Tester and Marshall 1961, Tester 1965, Vogl 1973.

Table 2.--Changes in density and trend of populations of breeding birds and mammals after burning (Bendell 1974)^{1/}

Foraging zone	Density			Trend		
	: Increase	: Decrease	: No Change	: Increase	: Decrease	: No Change
Birds, percentage						
Grassland and shrub	50	9	41	24	10	66
Tree trunk	28	16	56	4	8	88
Tree	24	19	57	6	6	88
Totals	35	15	50	12	8	80
Mammals, percentage						
Grassland and shrub	24	13	63	20	5	75
Forest	23	42	35	0	11	89
Totals	23	25	52	14	7	80

^{1/} See reference list for table 1.

While it is generally assumed that the beneficial aspects of fire are related to food production, there are many other considerations that may influence faunal relationships in burned habitat. In addition to modifying food production, burns create a mosaic of vegetation types (Daubenmire 1968, Heinzelman 1970, Vogl 1970), modify the supply of water (Adams et al. 1970, Ahlgren and Ahlgren 1960, Arnold 1963, Nieland 1958), and many produce specific kinds of habitat niches required by certain birds or mammals. Following fire, the concentration of plants near the ground should affect mammals more than birds, but a number of investigators have reported dramatic increases in mammals and seed-eating birds sometimes by ingress, when a burn produces large amounts of food (Edwards 1954, Munro and Cowan 1947, Ahlgren 1966, Cook 1959, Garman and Orr-Ewing 1949, Gashwiler 1970, Hagar 1960, Lawrence 1966).

Severe and repeated burning, however, may reduce reproduction of grasses, herbs and shrubs, and in turn, grazing and browsing wildlife (Darling 1960, Daubenmire 1968, Eddleman and McClean 1969, Penfound 1968, Van Wyk 1971, Leopold and Darling 1953, Dahlberg and Guettinger 1956, Scotter 1971, Vogl 1967).

In explaining post-fire response of birds and mammals, most investigators argue that quantity and quality of food are limiting for wildlife (Biswell et al. 1952, Dasmann 1971, Cringan 1958, Gullion 1967, Hagar 1960, Klein 1970, Komarek 1967, Leege and Hickey 1971, Watson and Moss 1972), and many investigators have shown increases in food production for ungulates on logged and burned areas (Gates 1968, Brown 1961, Dills 1970, Leege 1968, Leege and Hickey 1971, Lyon 1971, Reynolds 1962, 1964 and 1969, Pearson 1964 and 1968, Clary and Ffolliott 1966, Patton 1969, Clary and Larson 1971, Basile and Jensen 1971, Resler 1972, Ward 1973 and 1976). However, a number of biologists have also pointed out that there are no specific studies showing actual population increase as a result of these forage increases (Lyon 1971b, Allen 1971, Pengelly 1972).

There are many difficulties in evaluating the real importance of food to wildlife (Lack 1954, 1966 and 1970, Watson 1970, Chitty 1967, Dahlberg and Guettinger 1956, Hill 1971, Moss et al. 1971, Negus and Pinter 1966). Animal growth and condition may not provide adequate evaluation (Klein 1970, Watson and Moss 1972) and compensation by selective feeding and modified intake may reveal little relationship to animal welfare (Bissell 1959, Brown 1961, Crouch 1966, Gardarsson and Moss 1970, Miller 1968, Moss 1972, Pendergast and Boag 1971, Wood et al. 1962, Wynne-Edwards 1970, Hall 1971). However, some investigators (Grange 1949, Lauckhart 1957) believe that cycles in many herbivores may be caused by fire in the kind, quantity, and quality of food available.

Many investigators believe that the quality of food is the main factor limiting the abundance of herbivores (Batzli and Pitelka 1971, Klein 1970, Moss 1967, Schultz 1969, Watson and Moss 1972). After fires there is an impressive change in vigor of plants that may be caused by increased uptake of nutrients released in the ash (Ahlgren and Ahlgren 1960, Hayes 1970, Humphrey 1962, Komarek 1967, Trevett 1962, Vogl 1969). However, the level of nutrients in plants after burning may be unchanged, increased, or decreased, depending on season, soil, weather, fuels, the fire and other factors (Austin and Baisinger 1955, Beeson 1941, Daubenmire 1968, Einarsen 1946, Gessell and Balci 1963, Hayes 1970, Isaac 1963, Leege and Hickey 1971, Lemon 1968, Mayland 1967, Smith 1970, Wagle and Kitchen 1972, Allen et al. 1969, Aumann 1965). These complex relationships may explain why different burns may produce quite different kinds and numbers of wildlife.

Published results on nutritional quality of postfire forages and the effects on wildlife are, at best, not very informative. Increased nutrient levels in plants following fire may last from 1 to 20 years (Cowan et al. 1950, DeWitt and Derby 1955, Einarsen 1946, Gates 1968, Gimingham 1970, Trevett 1962, Mount 1969, Brown 1961). However, the level of increase for nitrogen (as protein) is only 1 to 2 percent, while phosphorous and magnesium are not much changed and calcium probably declines (Brown, 1961, DeWitt and Derby 1955, Einarsen 1946, Gates 1968, Lawrence and Biswell 1972, Lay 1957, Leege 1969, Leege and Hickey 1971, Taber and Dasmann 1958). When the ability

of animals to feed selectively is considered (Gullion 1970, Svoboda and Gullion 1972), the possible influence of nutritional changes is not very impressive.

Fire can have at least two completely different effects on water supplies available to wildlife--and both have been reported. Some fires improve the supply of free water by reducing the loss to vegetation and causing the water table to rise (Arnold 1963, Dasmann 1971, Ward 1968). Other fires may simply create such hot and dry conditions that the burned area becomes uninhabitable for at least part of the year (Dasmann 1971, Zwickel and Bendell 1967).

Mosaics in vegetation provide habitat diversity. A large fire could reduce the interspersions of food and cover for wildlife by producing a uniformity in vegetation. However, fires rarely burn evenly, and as a result often create a pattern of clumps of vegetation, burned logs and stumps, and open spaces (MacKay 1966, Heinselman 1970, Cooper 1961). Such cover patterns within a burn may determine where animals live and the densities they reach when specific habitat needs are developed (Bendell and Elliott 1966 and 1967, Martinka 1972, Watson and Moss 1972, Gullion and Marshall 1968, Miller 1964, Picozzi 1968). Clumped vegetation in a burn may also greatly influence predator-prey relationships by providing ambush cover for predators (Brynard 1971, Rusch and Keith 1971, Gullion 1967 and 1972).

Fires in old growth forests may create snags favorable to a wide variety of woodpeckers and hole nesting birds (Balda 1975, Bull 1974, Bull and Meslow 1977, Conner et al. 1975, McClelland 1977) and conversely, removal of snags by fire or felling may be a factor in the elimination of woodpeckers.

On a large scale, successive fires in the same habitat create abrupt edges (West 1971) and a variety of post-fire successional communities. The importance of edge and interspersions where two or more types come together had been reported as significant by many investigators (Biswell et al. 1952, Buckley 1958, Leopold 1933, Lovat 1911, McCulloch 1969, Gullion 1972), but nearly as many studies show no particular influence of edge on wildlife populations (Barick 1950, Gullion 1972, Bendell and Elliott 1966, Zwickel and Bendell 1972, Gates 1968).

Perhaps the real importance of vegetation interspersions created by fire is in maintaining a heterogeneity of environments--each of which will support a specific faunal community. Many studies have shown that different species of wildlife are associated with particular stages of vegetation growth (Brewer 1958, Grange 1948, Karr 1968, Martin 1960, Stelfox and Taber 1969, Franzreb 1977). The loss of a specific post-fire or post-logging successional stage may correlate with the decline of those species dependent on the particular vegetation represented. And, conversely, the maintenance of all successional stages through positive management should insure at least minimal levels of all potential species in an area (Thomas et al. 1976).

Heterogeneity of environments is also at least partially related to the size of burns or openings. Several investigators have noted that burns greater than 1,000 acres may be so large that animals will not move into them (Mount 1969, Biswell et al. 1952, Taber and Dasmann 1957, Robinson 1958). Recommended sizes of openings, however, vary widely, depending on the vegetation type and animal species involved (Biswell et al. 1952, Lyon 1976, Picozzi 1968, Gullion 1972, Robinson 1958).

In summarizing long-term influences of post-fire vegetal succession on faunal populations, no consistent generalizations are possible. Vegetation growth and change following fire provide the driving force for a dynamic system in which some species are favored, while others are not--and the balance changes continuously over time.

If we are to understand this dynamic system, we need research designed to describe the changes in vegetation and simultaneously determine the influence of vegetation composition and structure on faunal habitat requirements and populations.

EVOLUTION OF SPECIES IN A FIRE ENVIRONMENT

Many plant formations are flammable, and all or parts of them depend on repeated fire for their existence (Ahlgren and Ahlgren 1960, Daubenmire 1968, Flieger 1970, Heinselman 1971, Hodgson 1968, Kayll 1968, Komarek 1968, Lutz 1956, Mount 1964, Mutch 1970, Niering et al. 1970, Rowe 1970, Shafi and Yarranton 1973, Swan 1970, Thilenius 1968). A number of authors have pointed out that the fauna dependent on these fire habitats has evolved to exploit burned areas (Lemon 1968, Handley 1969, Wells 1965 and 1970, Miller 1963).

The relative stability of both species numbers and populations in burned environments has already been mentioned. This demonstration of adaptability by faunal species in fire environments also has some theoretical evolutionary implications. Undisturbed environments, such as tropical forests, tend to have a large number of species adapted to specific environmental niches that are stable and persistent (MacArthur et al. 1962, Orians 1969). Where habitats are frequently modified by fire, evolutionary selection may favor a few broadly adapted species rather than many specialists (Dunbar 1968, Shafi and Yarranton 1973, Martin 1960,. Unfortunately, fires tend to blur the separation of habitats and bring faunal species together--thus confounding the design for any test of the hypothesis (Speirs 1969 and 1972, Bendell 1955, King 1971, Johnsgard and Wood 1968).

In addition to the relatively larger size of birds (Bock and Lynch 1970, Martin 1960) and mammals in fire environments, different authors have listed such adaptations to fire as a lack of specialization on conifers (Udvardy 1969a), the ability to run or fly quickly and for long distances, burrowing, storing food, camouflage, pressing flat to avoid detection, migration, and some kinds of social display (Handley 1969, Komarek 1962, Bendell and Elliott 1966).

At the population level, species adaptations to a rapidly changing environment appear to include a high and variable birth rate and a high dispersal rate (Klein 1970, Klein and Strandgaard 1972, Geist 1971). Species with these characteristics can take immediate advantage of environmental changes.

KNOWLEDGE GAPS, RESEARCH NEEDS, AND PRIORITIES

Based on the review presented here, fire represents a dynamic and important force in the life histories of many faunal species. Our understanding of the role played by fire is weak in several areas, but the working group that prepared this review has identified two major gaps in our knowledge that appear to be of major importance and offer some probability of solution.

Ecosystem Response

We lack descriptions of both short-term and long-term ecosystem response to burning, including site-specific responses of food, cover, and animals, and differential response to season of burn and repeated burning.

We need general models of plant succession as affected by fire to predict site-specific community composition and structure over time. The research needed to develop these models is feasible and of high priority.

We need direct evaluation of animal population and behavioral changes caused by fire or other habitat modification. The research needed to accomplish this task is only partially feasible and of medium priority.

Species Relationships

We lack knowledge of specific habitat requirements, life histories, and inter-species relationships of key faunal species or groups.

We need to identify those animal species with: narrow ecological tolerance, major socioeconomic importance, and indicator values for groups of species. The research needed to complete this task is feasible and of high priority.

We need structural and compositional descriptors of optimal habitat for representative species or groups indicated above. The research needed to supply this information may be feasible in some cases and not in others but is of high priority.

SUMMARY AND CONCLUSIONS

Direct effects of fire on faunal populations vary widely. In general, while some evidence of vertebrate mortality has been reported, the most commonly held opinion is that vertebrates are rarely killed in fires and where death does occur it is usually negligible. Effects on invertebrate populations may

be short-term or long lasting. Numbers may decrease because the invertebrates or their eggs are killed, or their food supply and shelter are diminished. In some instances, populations of certain species that are attracted by heat, smoke, or damaged trees may increase during or after a fire.

The immediate post-fire environment presents all terrestrial fauna with a sudden and drastic modification of habitat structure and local microclimate. This may have positive or negative influences on various species. The most important effects of fire on stream fauna are related to loss of streamside vegetation and increased sediment load to the stream.

Long-term influences of post-fire vegetal succession on faunal populations cannot be generalized. Vegetation growth and change provide the driving force for a dynamic system in which some species are favored, while others are not.

Based on the state-of-knowledge review, fire represents a dynamic and important force in the life histories of many faunal species. Our understanding of the role played by fire is weak in several areas and requires additional research efforts.

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